

## Review of the genus *Acarterus* Loew from southern Africa, with description of seven new species (Diptera: Empidoidea; Hybotinae)

by

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### ABSTRACT

The southern Africa genus, *Acarterus* Loew (Diptera: Empidoidea; Hybotinae) is redefined to include the following: *A. unicolor* Loew, 3 undescribed species, and seven new species: *A. apicalis*, *A. darwini*, *A. londti*, *A. macrochaetus*, *A. nigricans*, *A. pallidus* and *A. stuckenbergi*. Phylogenetic analysis separated the species of *Acarterus* into a western Cape Province group and an eastern Highlands group. A key to species and illustrations of male and female terminalia are presented. Homologies of male terminalia in Hybotinae are discussed, and a key to the Afrotropical genera of Hybotinae, including *Chillcottomyia africana* (Smith), comb. n., is provided.

### INTRODUCTION

The Hybotinae of southern Africa are fairly well known, primarily as a result of the enormous contribution of Smith (1969). Previous to the present study, *Acarterus* Loew (Diptera: Empidoidea; Hybotinae) was a monotypic genus endemic to South Africa, confined to the southwestern region of the Cape Province (Smith 1969 1980). In the present study, additional material has resulted in the recognition of seven new species distributed over a much wider region of southern Africa.

This study was initiated following the discovery of two previously unknown specimens of Diptera collected by Charles Darwin during the voyage of the *Beagle*. The importance of these specimens was further augmented by their apparent uniqueness and difficulty in assigning them within any currently defined genus. They appeared similar to both *Syneches* Walker and *Acarterus*, and the exact determination was further hampered by the absence of antennae. Specimens congeneric with the Darwin species were later discovered in the Natal Museum, and detailed examination of the male terminalia enabled me to confirm that all species were congeneric in an expanded definition of *Acarterus* (see 'Recognition' under *Acarterus*).

### MATERIALS AND METHODS

**Materials:** This study was based on 53 pinned specimens of *Acarterus* found in the following institutions: The Natural History Museum, London, England (BMNH); Natal Museum, Pietermaritzburg, South Africa (NMSA); Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS). Several voucher specimens are housed in the Canadian National Collection, Ottawa (CNC).

**Descriptive format:** Label data of holotypes are cited in full, with original spelling,

punctuation and date; lines are delimited by a slash mark(/). A semicolon separates data quoted from different labels.

Terms and structures: Terms used for adult structures follow those of McAlpine (1981), except male terminalia where terms of Cumming *et al.* (1995) are followed. There are several new genitalic structures or configurations that are possibly derived within the Hybotine-group of subfamilies as compared to the ground plan of the Empidoidea, and consequently the terminalia of *Acarterus* are discussed in more detail below.

The terminalia of *Acarterus* are asymmetrical with a deeply emarginate epandrium and partially articulated surstyli. The phallus is simple and similar to *Trichinomyia* Tuomikoski (Cumming *et al.* 1995, fig. 12a), *Hoplocyrtoma* Melander, and many Oedaleini (Chvála 1983, fig. 460). It consists of a long ejaculatory apodeme fused to a hood-like open tube (Figs 23 & 25). The hypandrium in *Acarterus* is a shallow, concave plate with a pair of posterior processes. Apical hypandrial processes are common in the Hybotinae and related subfamilies; e.g. *Bicellaria* Macquart (Fig. 29) and *Oedalea* Meigen (Chvála 1983, figs 323, 403).

Surrounding the phallus are a pair of asymmetrical lobes that are of uncertain origin. Chvála (1983) referred to them as 'postgonites', but did not discuss their origin. In addition, there is a 'V'-shaped rod beneath the ejaculatory apodeme, termed here the ventral apodeme (Figs 25, 26, 29). The derivation and origin of these two terms can be traced through the examination of other genera of Hybotinae (*Lamachella* Melander, *Stenoproctus* Loew), Oedaleini (*Euthyneura* Macquart, *Oedalea*), and Ocydromiinae (*Bicellaria*; Figs 26–29; Chvála 1983, figs 318–320). The postgonites are formed from processes arising from the dorsolateral margin of the hypandrium, on either side of the phallus (Figs 27, 29). These processes are fused laterally by a narrow connection to the hypandrium in genera such as *Bicellaria* and *Lamachella* (Figs 27, 29) or have become articulated as in *Acarterus* and *Stenoproctus* (Fig. 28). This transformation from simple to complex articulated lobes demonstrates that postgonites *sensu* Chvála are hypandrial in origin.

The inner walls of the postgonites extend anteriorly, parallel to the phallus, and fuse together ventrally beneath the phallus and ejaculatory apodeme (Figs 23, 26, 28). This structure forms a ventral supportive brace or ventral apodeme beneath the phallus and is also hypandrial in origin. The ventral apodeme in *Acarterus* is long and robust, forming a 'V'-shaped apodeme, ventral to the ejaculatory apodeme (Figs 11, 23, 25). The ventral apodeme appears to be homologous to the second apodeme that is present in most genera of the Tachydromiinae as discussed by Cumming & Cooper (1992).

#### TAXONOMY

##### Key to the Afrotropical genera of Hybotinae (modified from Smith 1969)

- 1 Cell cup longer or almost as long as cell bm, apex convex or pointed .....2
- Cell cup much shorter than cell bm, apex truncate or square .....7
- 2 Vein Rs short, arising distal to middle of cell bm .....3

- Vein Rs long, arising basal to middle of cell bm.....4
- 3 Basal section of M (separating basal cells br and bm) very faint ....**Syndyas** Loew  
(includes *Sabinios* Garrett Jones, see Chvála 1975)
- Basal section of M distinct.....**Hybos** Meigen
- 4 Proboscis short, fleshy and directed downwards; hind basitarsis swollen .....5
- Proboscis long, rigid and directed forwards; hind basitarsis slender .....6
- 5 Cell cup longer than cell bm; CuA<sub>2</sub> meeting A<sub>1</sub> at acute angle ...**Afrohybos** Smith
- Cell cup subequal in length to cell bm; CuA<sub>2</sub> meeting A<sub>1</sub> at nearly right angles .....Undescribed genus  
(specimens in CNC, BMNH)
- 6 First flagellomere conical (Fig. 7); arista short, slightly shorter to nearly twice length of first flagellomere; proboscis very slender with a small, yet distinct labellum with pseudotracheae; head round, not flattened anteriorly above .....**Acarterus** Loew
- First flagellomere short ovate; arista long, more than four times length of first flagellomere; proboscis with wide base, labellum rigid, pseudotracheae absent; head distinctly flattened anteriorly above .....**Syneches** Walker
- 7 Eyes pubescent .....**Chillcottomyia** Saigusa  
(see below)
- Eyes bare .....8
- 8 Vein Rs arising beyond middle of cell bm .....**Lamachella** Melander
- Vein Rs arising basal to middle of cell bm .....**Stenoproctus** Loew

#### *Chillcottomyia* Saigusa

*Chillcottomyia* was erected for a group of *Stenoproctus*-like flies with slender hind femora and pilose eyes (Saigusa 1986). The generic concept was first tentatively suggested by Smith (1965) for *Stenoproctus nepalensis* Smith. In his revision of southern Africa Empididae, Smith (1969) described an additional species, *Stenoproctus africanus*, which he considered closely resembled the Nepal species on the basis of slender hind femora. Saigusa (1986) did not transfer the latter species to *Chillcottomyia*, because the presence of pilose eyes could not be confirmed. Following the examination of the holotype and an additional South African female of this species in the Natal Museum (Eastern Cape Province: Otterford Forestry Reserve, Hankey area, 1–10.12.67, 3325CC, B. & P. Stuckenberg), I am able to confirm that the eyes are densely pilose. Consequently, *Stenoproctus africanus* should be transferred to *Chillcottomyia*, and is here listed as *Chillcottomyia africana* (Smith), **comb. n.** In addition to southern Africa, *Chillcottomyia* is known from Nepal, Japan, Taiwan, and the Philippines (Saigusa 1986).

#### *Acarterus* Loew

*Acarterus* Loew, 1858: 340 [1860: 334]. Type species: *Acarterus unicolor* (monotypy).

Recognition: *Acarterus* is characterised by a long, slender proboscis and truncate cell cup, equal in length to cell bm. It is distinguished from *Syneches* by a conical first

flagellomere, arista slightly shorter to nearly twice the length of the first flagellomere, proboscis long and slender with a small labellum bearing pseudotracheae, and male terminalia with long, apical, asymmetrical hypandrial lobes, 'V'-shaped ventral apodeme, and pair of asymmetrical postgonites.

**Description (male):** *Head* (Fig. 7): Spherical, not flattened anteriorly above; first flagellomere conical, with short pruinescence; arista slightly shorter to nearly twice length of first flagellomere. Eyes contiguous above, upper ommatidia enlarged. Proboscis very slender with a small, distinct labellum with pseudotracheae; palpi linear, slender and obliquely directed, with several long setae.

*Thorax*: Not greatly convex; notopleurals in oblique row; scutum with rows of short to long acrostichal and dorsocentral setae; scutellar setae numerous, inner apical pair often slender and short, flanked by pair of stout, long setae; proepisternum with setae anterior to spiracle and above fore coxae; laterotergite bare.

*Legs* (Fig. 8): Hind femur slender or thickened, bearing long or spine-like setae. Hind tibia subequal to distinctly shorter than femur.

*Wing* (Figs 30 & 31): Completely clothed in microtrichia; stigma usually elongate, faint to dark; Sc incomplete, fading prior to C; Rs arising basal to middle of cell br;  $R_1$  usually straight;  $R_{2+3}$  and  $R_{4+5}$  diverging;  $R_{4+5}$  unbranched;  $R_{4+5}$  and  $M_1$  parallel at wing margin; cell dm longer than basal cells; remnant of  $M_2$  sometimes visible on margin of cell dm; apex of cell cup truncate, not projecting beyond cell bm;  $A_1$  faint, extending to wing margin.

*Abdomen*: Long setae often on both lateral and ventral surfaces. Terminalia (Figs 22–25) asymmetrical, rotated between 45–90° to right. Cerci short, slender, lightly sclerotised. Surstyli usually bare, lacking microtrichia, surface polished. Hypandrium divided apically into pair of asymmetrical lobes bearing long stout setae. Phallus with hood-like tubular apex, ventral margin separated by seam; ejaculatory apodeme slender, extending to fusion of 'V'-shaped ventral apodeme. Postgonites asymmetrical with ventrolateral setae; usually left postgonite arched dorsally over phallus; right postgonite slender.

**Female**: Similar to male except as follows: Abdominal segments 1–5 broad; segments 6–10 narrow, tapering to pair of short cerci (Fig. 9). Spermatheca not visible.

**Remarks**: Adults of *Acarterus* inhabit grasslands and low shrubs. Species of *Acarterus* (*londti*) have been collected from the macchia vegetation which dominates the southwestern Cape Province. Although unknown, the immature stages are probably terrestrial.

Adults of the Hybotinae mate on the ground and do not form aerial mating swarms (Chvála 1976). Holoptic eyes are present in both sexes and are presumed to be adapted for hunting flying insects, attacking the prey from below. Although hybotines are assumed to be predacious, the long, slender proboscis suggests that adults of *Acarterus* may visit flowers. However, in the absence of detailed observations this remains speculative. If *Acarterus* is associated with flowers, then species are presumably nectar feeders, because pollen was not observed in the gut.

Key to the species of *Acarterus* Loew

- 1 Hind femora not thickened, similar to middle femora, with long slender anteroventral setae; hind tibiae subequal in length to hind femora.....2
  - Hind femora thickened compared to middle femora, with numerous stout or spine-like setae beneath and apically; hind tibiae shorter than hind femora.....6
- 2 Halter pale, legs concolorous with thorax .....sp. 3
  - Halter dark, concolorous with thorax; if halter pale, legs yellowish-brown and thorax dark .....3
- 3 Legs yellowish-brown, thorax dark; surstyli clothed with microtrichia, not bare and shiny .....**pallidus** sp. n.
  - Legs dark, concolorous with thorax; surstyli bare and shiny, lacking microtrichia .....4
- 4 Thoracic setae long and stout; right hypandrial process strongly constricted at base .....**macrochaetus** sp. n.
  - Thoracic setae short and slender; right hypandrial process not strongly constricted at base .....5
- 5 Uniserial dorsocentral setulae; setulae on either side of prescutellar depression lacking; thorax less robust; process at base of right surstylus lacking.....
 

**unicolor** Loew

  - Biserial dorsocentral setulae; one pair of setulae on either side of prescutellar depression; thorax robust; short process at base of right surstylus .....
 

**nigricans** sp. n.
- 6 First flagellomere more than twice as long as pedicel and scape combined; halter pale in male, dark in female.....**apicalis** sp. n.
  - First flagellomere at most twice as long as pedicel and scape combined; halter variable in colour.....7
- 7 Halter pale, not concolorous with thorax.....**stuckenbergi** sp. n.
  - Halter dark, concolorous with thorax.....8
- 8 Tibiae dark, concolorous with femora .....sp. 2
  - Tibiae pale, orange-brown.....9
- 9 Hind femora orange-brown with dark, apical band.....sp. 1
  - Hind femora orange-brown to dark brown, lacking dark apical band .....1 0
- 10 Coxae dark, concolorous with thorax.....**londti** sp. n.
  - Coxae pale, distinctly more lightly pigmented than thorax .....**darwini** sp. n.

***Acarterus apicalis* sp. n.**

Figs 1–4

*Etymology:* *Apiculus* (L.) = apex. Refers to the dark band on the apex of the hind femora.

Holotype ♂: SOUTH AFRICA: *Cape Province*: 'Zuurberg Range/ north of Addo/ E. Cape Prov./ South Africa/ 10 April 1961/ collectors/ B. & P. Stuckenberg' [dissected]; 'HOLOTYPE/ *Acarterus/ apicalis/ Sinclair*' [red label]. In NMSA.

**Recognition:** Distinguished from other species of *Acarterus* by the very long first flagellomere, bright orange coxae, shiny pleura, and the dark apical band on the hind femur.

**Description (male):** Wing length 3.4 mm.

**Head:** First flagellomere more than twice as long as pedicel and scape combined; arista slightly longer than first flagellomere (Fig. 4). Proboscis slightly longer than height of head.

**Thorax:** Clothed in pruinescence, except proepimeron, anepisternum, katapisternum, and anepimeron; apex of postpronotal lobe pale; vittae lacking. Acrostichal setulae in 2 rows of 2; dorsocentral setulae uniserial, with 2 postsutural dorsocentral setae; intra-alar setulae lacking; 1 presutural and 1 postsutural inter-alar setae; 1 postpronotal, with several long setulae; 2–3 notopleurals; 1 postalar; 1 pair of stout and 2 pairs of slender scutellar setae. Antepronotum with row of short setae. Halter brown.

**Legs:** Coxae, trochanters, femora, fore and mid tibiae yellowish-orange; hind femur with dark apical band, posterior surface with setae; hind tibiae and tarsomeres brown. Tibiae with long, dark setae. Hind femur 1.5 X longer than mid femur and thickened; 2–3 pre-apical anterodorsal stout setae; multiple rows of black spine-like setae beneath, increasing in length apically. Hind tibia geniculate, shorter than femur, ventral surface arched along margin of femur, apex slightly swollen. Hind coxae inflated, wider than fore or mid coxae.

**Wings:** Stigma nearly round;  $R_1$  deflected beneath stigma; remnant of  $M_1$  visible only as crease;  $CuA_1$  slightly longer than crossvein  $dm-cu$ ;  $CuA_2$  convex, meeting  $A_1$  at obtuse angle.

**Abdomen:** Lateral and ventral margins clothed in long, silky white setae; sclerites brown, lacking band of silver pruinescence.

**Terminalia (Figs 1–3):** Epandrium asymmetrical; right surstylus slender, tapering to point; short lobe at base of right surstylus absent; left surstylus gradually tapered; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe long, narrow, longer than left lobe; left hypandrial lobe triangular, tapered; each lobe bearing a long, stout apical seta. Left postgonite with apex expanded dorsally over phallus; right postgonite slender with round apex.

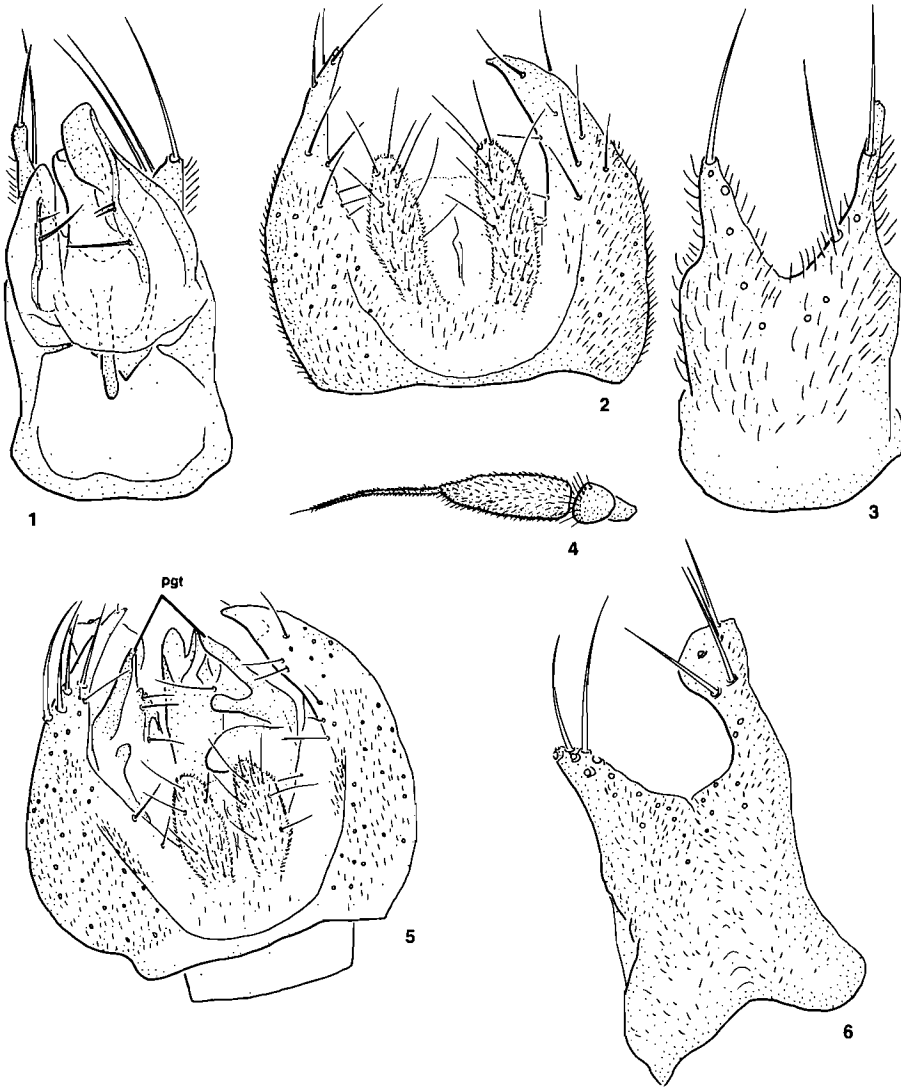
**Female:** Similar to male except halter pale. Terminalia as in generic description.

**Additional material:** SOUTH AFRICA: *Cape Province*: Paratype: 1 ♀, same data as holotype (NMSA).

**Remarks:** The very long first flagellomere differs from that of all other species of *Acarterus*.

This species is isolated from all other *Acarterus*, and is found northeast of Port Elizabeth (Fig. 32). The Suurberg Range constitutes the easternmost occurrence of the Cape Fold Mountains and of the Fynbos Floral Biome. The area is transitional from a zone of perennial rains in the west to summer rains in the east. The flora is consequently mixed, with elements of the fynbos (the typical flora of the Fold Mountains in the southern and southwestern Cape) and also grassland. As a consequence of edaphic, climatic and topographic features, the Suurberg is an

ecological island, isolated by the surrounding Savannah Biome and an eastern extension of the Nama-Karoo Biome (Rutherford & Westfall 1994, Cowling & Richardson 1995). This favours endemism in the insect fauna.



Figs 1–6. *Acarterus* species, male terminalia and antenna. 1–4. *A. apicalis* sp. n. 1. Hypandrium, postgonites and phallus, dorsal view. 2. Epandrium and cerci, dorsal view. 3. Hypandrium, ventral view. 4. Antenna. 5–6. *A. darwini* sp. n. 5. Terminalia, dorsal view. 6. Hypandrium, ventral view. [Abbreviation: pgt = postgonite.]

***Acarterus darwini* sp. n.**

Figs 5, 6

*Etymology*: Named in honour of Charles Darwin, who collected the only known specimens of this species (see 'Remarks' below).

*Holotype* ♂: SOUTH AFRICA: *Cape Province*: 'Cape of Good Hope, C. Darwin.'; 'Darwin coll./ 1885-119' [= BMNH Accession number 119 in the year 1885]; 'Cape/ 3690' [hand written]; '3690' [hand written]; 'HOLOTYPE/ *Acarterus/ darwini/ Sinclair*' [red label] [dissected]. In BMNH.

*Recognition*: Very similar to *A. londti*, but distinguished by the pale coxae, shorter proboscis, four rows of acrostichal setulae, and lack of a short process at the base of the right surstylus.

*Description* (male): Wing length 4.7 mm.

*Head*: Antennae damaged, missing first flagellomere and arista. Proboscis subequal in length to height of head.

*Thorax*: Clothed in grey pruinescence, except apex of postpronotal lobe pale; pair of silver vittae separating acrostichal and dorsocentral setulae. Acrostichal setulae in 4 rows; dorsocentral setulae biserial, expanding to 3 postsutural rows of long, stout setae; intra-alar setae long, confined to presutural and postsutural patches; 1 stout seta and 10 long, slender postpronotal setae; 4 notopleurals; 1 postalar; 5 pairs scutellar setae, with slender setae interspersed. Anteprenotum with row of long, stout setae. Halter pale, concolorous with femora.

*Legs*: Coxae and trochanters pale, distinctly more lightly pigmented than thorax; femora completely orange, posterior surface with setae; tibiae, first and second tarsomeres orange, remaining tarsomeres dark. Tibiae with long, dark setae. Hind femur 1.5 X longer than mid femur and thickened; apical half with row of anterodorsal spine-like setae; multiple rows of black spine-like setae beneath, increasing in length apically. Hind tibia geniculate, shorter than femur, ventral surface straight, apex slightly swollen. Hind coxae inflated, wider than fore or mid coxae.

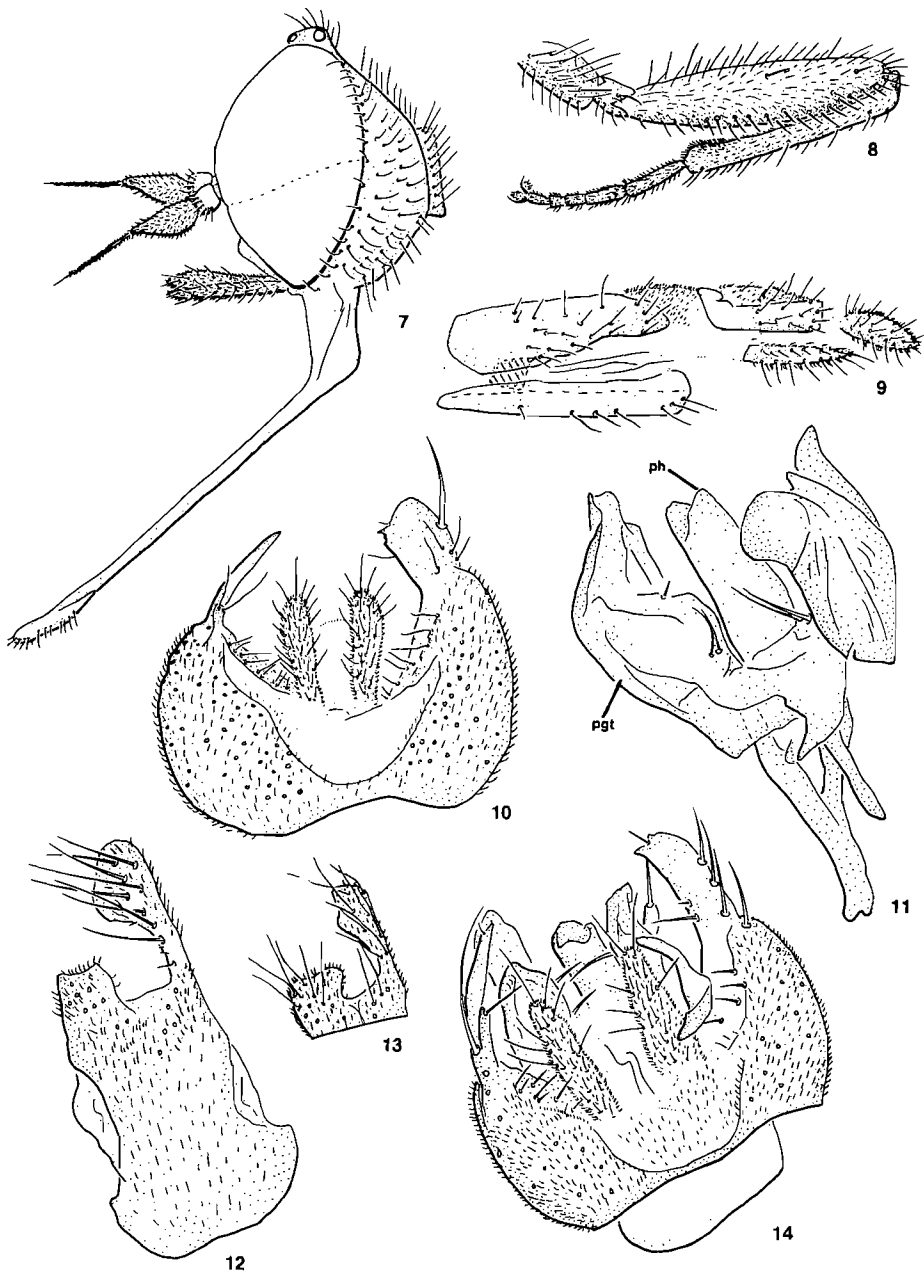
*Wings*: Stigma faint, elongate; R<sub>1</sub> straight; remnant of M<sub>1</sub> lacking; CuA<sub>1</sub> half length of crossvein dm-cu; CuA<sub>2</sub> more or less straight, meeting A<sub>1</sub> at right angle.

*Abdomen*: Lateral and ventral margins clothed in long, dark setae; concolorous with thorax, dusty with grey pruinescence; posterodorsal margins lacking band of silver pruinescence.

*Terminalia* (Figs 5, 6): Right surstylus tapering to truncate apex; base of right surstylus lacking short lobe; left surstylus broad, strongly tapered on apical fifth, ventral surface of apex with ridge; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe with narrow base, expanding apically, more than twice length of left hypandrial lobe; left hypandrial lobe short, truncate, sometimes expanded mediolaterally. Left postgonite with pair of broad lateral processes, extending dorsally over phallus, posterior process bilobed; right postgonite with slender apex.

*Female*: Similar to male except for abdomen. See generic description.





Figs 7–14. *Acarterus* species, male and female terminalia, head and hindleg. 7–13. *A. londti* sp. n. 7. Head, profile. 8. Hindleg, anterior view. 9. Female terminalia. 10. Epandrium and cerci. 11. Phallus and postgonites. 12. Hypandrium (Locality: Pringle Bay), ventral view. 13. Apex of hypandrium (Locality: Sevenweekspoort), ventral view. 14. *A. macrochaetus* sp. n., terminalia, dorsal view. [Abbreviations: pgt = postgonite; ph = phallus.]

Additional material: SOUTH AFRICA: *Cape Province*: Paratype: 1 ♀, same data as holotype (BMNH).

Remarks: The only two specimens known of this species were collected by Charles Darwin during the voyage of the *Beagle* and were found while sorting the accessions collection at the Natural History Museum in London (BMNH). They apparently had been overlooked and are in good condition, mounted laterally on cards, only missing their antennae.

The number '3690' links the specimens directly to Darwin's *Insect Notes*. This is a set of handwritten field notes and localities cataloguing the specimens collected during his voyage. According to the number, the specimens were among 'small insects sweeping in valleys of mountains near Simons Bay [Cape Province, South Africa], June [1836]' (Fig. 32) (Smith 1987 1996). Prior to the discovery of these two specimens, only Hemiptera, Coleoptera and Tachinidae were among Darwin's collections from this locality (Smith 1987). Neither of the handwritten labels is in Darwin's own hand (Smith, *pers. comm.*).

### ***Acarterus londti* sp. n.**

Figs 7–13, 30

*Etymology*: Named in honour of the collector of the holotype.

Holotype ♂: SOUTH AFRICA: *Cape Province*: 'South Africa : Cape/ Pringle Bay 3418BD/ 22.ix.1979/ J. Londt/ Swept veget. nr. sea'; 'HOLOTYPE/ *Acarterus/ londti/ Sinclair*' [red label]. In NMSA.

Recognition: Distinguished from other species of *Acarterus* by the dark coxae and the bright orange to dark brown legs, which lack distinct apical bands. Male terminalia with short process at base of right surstylus and short truncate left hypandrial process.

Description (male): Wing length 3.5–4.7 mm.

*Head* (Fig. 7): First flagellomere twice as long as pedicel and scape combined; arista slightly less than twice length of first flagellomere. Proboscis variable in length, 1.33–1.67 X longer than height of head.

*Thorax*: Clothed in grey pruinescence, except apex of postpronotal lobe pale; pair of silver vittae separating acrostichal and dorsocentral setulae. Acrostichal setulae in 8 rows, reduced to 4 rows posteriorly; dorsocentral setulae in 8 rows, reduced to 3 rows of 3–5 postsutural dorsocentral setae; intra-alar setulae in 3–4 rows; 1 postpronotal, with many long, fine setae; 3–4 notopleurals; 1 postalar; 4–5 pairs scutellar setae, with slender setae interspersed. Anteprenotum with row of long setae. Halter yellow.

*Legs*: Coxae and trochanters dark, with grey pruinescence; femora completely orange to concolorous with coxae, posterior surface with setae; tibiae, first and second tarsomeres orange, remaining tarsomeres dark. Tibiae with long, dark setae. Hind femur 1.5 X longer than mid femur and thickened (Fig. 8); apical half with row of anterodorsal spine-like setae; multiple rows of black spine-like setae beneath, increasing in length apically. Hind tibia geniculate, shorter than femur, ventral

surface arched along margin of femur, apex slightly swollen. Hind coxae inflated, wider than fore or mid coxae.

**Wings** (Fig. 30): Stigma distinct, elongate;  $R_1$  straight; remnant of  $M_1$  often visible as a short vein or crease;  $CuA_1$  shorter than crossvein  $dm-cu$ ;  $CuA_2$  slightly sinuous, meeting  $A_1$  at acute angle.

**Abdomen**: Lateral and ventral margins clothed in long, silky white setae; concolorous with thorax, dusty with grey pruinescence; posterodorsal margins with band of silver pruinescence.

**Terminalia** (Figs 10–13): Right surstylus very slender, tapering to point; base of right surstylus with short, truncate lobe, bearing several setae; left surstylus dorsoventrally flattened, apex rounded, with 2–3 subapical lateral teeth; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe with narrow base, expanding apically; left hypandrial lobe short, truncate, less than half length of right lobe. Left postgonite with broad lateral process, extending dorsally over phallus; right postgonite with broad base, apex truncate.

**Female**: Similar to male except for abdomen. See generic description.

**Additional material**: SOUTH AFRICA: *Cape Province*: Paratypes: 3♂1♀, same data as holotype (NMSA); 2♂2♀, Bainskloof, Wellington Distr., 2000', 4–5.x.1959, B. & P. Stuckenberg (CNC, NMSA); 1♀, Du Toits Kloof, Paarl Distr., West Cape, 2000–3500', 27–28.ix.1959, B. & P. Stuckenberg (NMSA); 2♀, Franschhoek Pass, nr. Franschhoek, West Cape, 7–8.x.1959, B. & P. Stuckenberg (CNC, NMSA); 1♂, Pakhuis Pass, Clanwilliam Distr., SW Cape, 17–19.x.1964, B. & P. Stuckenberg, 950m (BMNH); 2♂, Sevenweekspoort, Laingsburg Dist., West Cape, 19–22.ix.1959, B. & P. Stuckenberg (NMSA). 1♂1♀ paratype deposited in CNC.

**Remarks**: This species ranges from sea level to almost 1000 m (Fig. 33) and has been collected in early spring (September–October). All localities for this species are within the Fynbos Biome of the Cape Floral Kingdom. Most of them are in passes through various ranges of the Cape Fold Mountains. The characteristic flora is sclerophyllous Montane Fynbos shrubland typical of these sandstone and quartzite mountains (Moll *et al.* 1984).

Despite the external similarities in size and colour, the phylogenetic analysis suggests that *A. londti* and *A. darwini* are distantly related based on the male terminalia (see Phylogenetic Considerations).

### ***Acarterus macrochaetus* sp. n.**

Figs 14, 15

**Etymology**: *Makros* (Gr.) = long. Refers to the long, stout thoracic setulae of this small, black species.

**Holotype** ♂: SOUTH AFRICA: *Cape Province*: 'Cape Province./ Swellendam./ ii.1932.'; 'S. Africa./ R.E.Turner./ Brit. Mus./ 1932-145.' [dissected]; 'HOLOTYPE/ *Acarterus/ macrochaetus/ Sinclair*' [red label]. In NMSA.

**Recognition**: Distinguished from both *A. nigricans* and *A. unicolor* by long, stout thoracic setulae, a slender process at the base of the right surstylus, and a narrow left surstylus.

Description (male): Wing length 2.3 mm.

*Head*: First flagellomere twice as long as pedicel and scape combined; arista slightly longer than first flagellomere. Proboscis subequal in length to height of head.

*Thorax*: Brown, including apex of postpronotal lobe; dusted with pruinescence; vittae lacking. Setulae long and stout; acrostichal setulae in 4 rows, 1 pair of long setae on either side of prescutellar depression; dorsocentral setulae with 2 presutural rows, and 2 postsutural dorsocentral setae; intra-alar setulae in 3–4 rows; 1 postpronotal, with many long, fine setae; 4 notopleurals; 1 postalar; 4–5 pairs scutellar setae. Anteprenotum with row of long setae. Halter dark.

*Legs*: All leg segments brown to black, lacking stout setae. Tibiae with several long setae. Hind femur slightly longer than mid femur, not thickened; anteroventral margin with row of setae. Hind tibia straight, subequal in length to femur, apex not swollen. Hind coxae subequal in width to mid coxae.

*Wings*: Stigma distinct, elongate;  $R_1$  straight; remnant of  $M_1$  not visible;  $CuA_1$  slightly longer than crossvein dm-cu;  $CuA_2$  convex, meeting  $A_1$  at right angle.

*Abdomen*: Lateral margin with long, dark setae; concolorous with thorax, dusty with grey pruinescence; lacking bands of pruinescence.

*Terminalia* (Figs 14, 15): Right surstylus slender, tapering to sharp tip bearing short, subapical, peg-like seta; right surstylus with long, narrow basal lobe, bearing single seta; left surstylus dorsoventrally flattened, apex rounded, with 2 subapical teeth and single long setula; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe with narrow base and expanded apex, one-third longer than left lobe; left hypandrial lobe narrow, with broad base tapering to round apex. Left postgonite with pair of slender lateral processes extending dorsally over phallus; right postgonite broad.

Female: Unknown.

Remarks: This species is based on specimens collected in summer, in contrast to other species of *Acarterus* from the western Cape Province which are known from spring and winter.

### ***Acarterus nigricans* sp. n.**

Figs 16, 17, 31

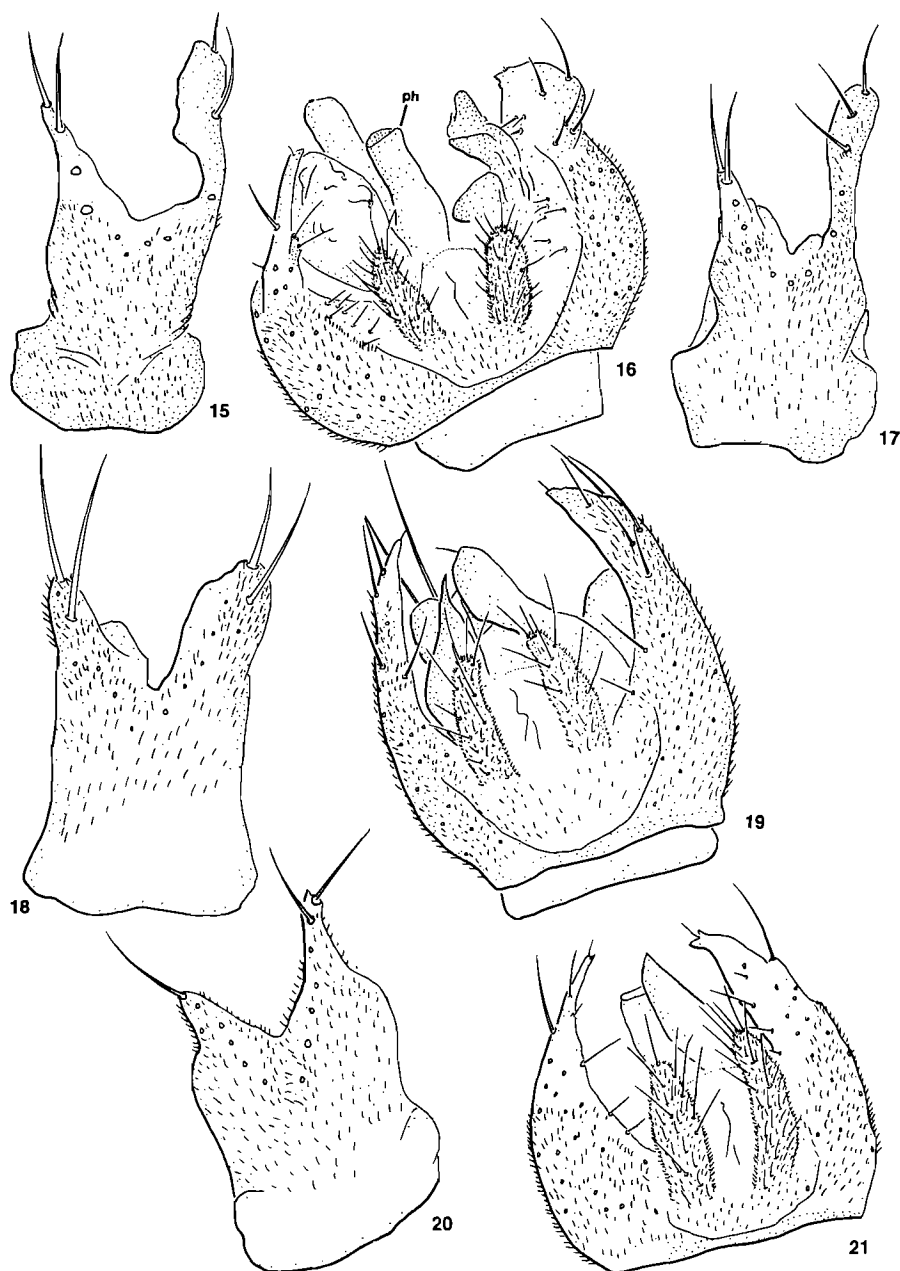
*Etymology*: *Nigricans* (L.) = blackish. Refers to the dark thorax and abdomen.

Holotype ♂: SOUTH AFRICA: *Cape Province*: 'Cape Province./ Robertson [Robinson?] Pass./ Nr. Mossel Bay./ 2000ft.4.ix.1932'; 'S. Africa./ R.E.Turner./ Brit. Mus./ 1932-421.'; 'HOLOTYPE/ *Acarterus/ nigricans/ Sinclair*' [red label]. In BMNH.

Recognition: Externally most similar to *A. unicolor*, but differs in having biserial dorsocentral setulae, one pair of setulae on either side of prescutellar depression and a more robust thorax. This species is only confidently distinguishable from *A. unicolor* based on the male terminalia.

Description (male): Wing length 2.25–2.3 mm.

*Head*: First flagellomere twice as long as pedicel and scape combined; arista slightly



Figs 15–21. *Acarterus* species, male terminalia. 15. *A. macrochaetus* sp. n., hypandrium, ventral view. 16–17. *A. nigricans* sp. n. 16. Terminalia, dorsal view. 17. Hypandrium, ventral view. 18–19. *A. pallidus* sp. n. 18. Hypandrium, ventral view. 19. Terminalia, dorsal view. 20–21. *A. stuckenbergi* sp. n. 20. Hypandrium, ventral view. 21. Epandrium, phallus and postgonite, dorsal view. [Abbreviation: ph = phallus.]

shorter to slightly longer than first flagellomere. Proboscis subequal in length to height of head.

**Thorax:** Black, including apex of postpronotal lobe; dusted with pruinescence; vittae lacking. Setulae short; acrostichal setulae in 4 rows, 1 pair of long setae on either side of prescutellar depression; dorsocentral setulae biserial, with 2 postsutural dorsocentral setae; intra-alar setulae in 3–4 rows; 1 postpronotal, with many long, fine setae; 3–4 notopleurals; 1 postalar; 4–5 pairs of scutellar setae. Anteprenotum with row of long setae. Halter dark.

**Legs:** All segments brown to black, lacking stout setae. Tibiae with several long setae. Hind femur slightly longer than mid femur, not thickened; anteroventral margin with row of long setae. Hind tibia straight, subequal in length to femur, apex not swollen. Hind coxae subequal in width to mid coxae.

**Wings (Fig. 31):** Stigma distinct, elongate;  $R_1$  straight; remnant of  $M_1$  not visible;  $CuA_1$  at most twice length of crossvein dm-cu;  $CuA_2$  convex, meeting  $A_1$  at right angle.

**Abdomen:** Lateral margin with long, dark setae; concolorous with thorax, dusty with grey pruinescence; lacking bands of pruinescence.

**Terminalia (Figs 16, 17):** Right surstylus slender, tapering to blunt tip bearing short, subapical, peg-like seta; right surstylus with short basal lobe, bearing 2 setae; left surstylus dorsoventrally flattened, apex rounded, with 3 subapical lateral teeth and several peg-like setulae; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe slightly arched with expanded apex, nearly twice length of left lobe; left hypandrial lobe short, with broad base tapering to round apex. Left postgonite with pair of triangular lateral processes extending dorsally over phallus; right postgonite broad.

**Female:** Similar to male except for abdomen. See generic description.

**Additional material:** SOUTH AFRICA: *Cape Province:* Paratypes: 3♂2♀ 1?, same data as holotype. 1♂1♀ paratypes deposited in NMSA.

### ***Acarterus pallidus* sp. n.**

Figs 18, 19

**Etymology:** *Pallidus* (L.) = pale. Refers to the pale legs.

**Holotype** ♂: LESOTHO: 'Blue Mountain Pass/ Makhaleng Valley/ Maloti Mountains/ 2150–2525m./ 12–14 Jan. 1963'; 'Maseru District/ Basutoland/ B. & P. Stuckenberg'; 'HOLOTYPE/ *Acarterus/ pallidus/ Sinclair*' [red label]. In NMSA.

**Recognition:** Distinguished from all species of *Acarterus* with slender hind femora by its pale legs. The surstyli are clothed with microtrichia and not bare and shiny as found in all other species of *Acarterus*.

**Description (male):** Wing length 2.7–3.1 mm.

**Head:** First flagellomere twice as long as pedicel and scape combined; arista 1.5 times to nearly twice length of first flagellomere. Proboscis slightly longer than height of head.

**Thorax:** Brown, apex of postpronotal lobe yellowish-brown; dusted with

pruinescence; vittae lacking. Setulae short; acrostichal setulae in 4 rows, 1 pair of setae on either side of prescutellar depression; dorsocentral uniserial, with 2 postsutural dorsocentral setae; 3 intra-alar setulae; 1 postpronotal, with several fine setulae; 3 notopleurals; 1 postalar; 3 pairs scutellar setae. Anteprenotum with row of long setae. Halter dark.

Legs: All segments yellowish-brown, darker on apical segments, lacking stout setae. Tibiae with several long setae. Hind femur 1.25 X longer than mid femur, not thickened; anteroventral margin with row of long setae. Hind tibia straight, subequal in length to femur, apex swollen. Hind coxae subequal in width to mid coxae.

Wings: Stigma distinct, elongate;  $R_1$  straight; remnant of  $M_1$  not visible;  $CuA_1$  slightly longer than crossvein dm-cu;  $CuA_2$  convex, meeting  $A_1$  at obtuse angle.

*Abdomen*: Lateral and ventral margins with long, pale, silky setae; concolorous with thorax, dusty with grey pruinescence; lacking bands of pruinescence.

*Terminalia* (Figs 18, 19): Right surstylus narrow, tapering to blunt tip with short apical setulae; right surstylus lacking basal lobe; left surstylus broad, tapering, bearing single apical setula; surstyli clothed with microtrichia, except for apex. Right hypandrial lobe broad, parallel-sided with broadly rounded apex, slightly longer than left lobe; left hypandrial lobe with broad, expanded base, tapering to round apex. Left postgonite with expanded apex, extending dorsally over phallus; right postgonite slender and pointed.

Female: Unknown.

Additional material (collected by B. & P. Stuckenberg): LESOTHO: Paratype: 1♂, same data as holotype. SOUTH AFRICA: *Cape Province*: 2♂, Naude's Nek, Barkly East Dist., East Cape Prov., 19 Jan. 1963, 2350–2525m (NMSA).

*Remarks*: The dominant vegetation of the type locality is Afro-alpine montane grassland (Killick 1978). The collecting site at Naude's Nek is illustrated by Smith (1969, fig. 419); the photograph shows the zonation of hygrophilous plants surrounding a small marsh, where the specimens were collected.

There is an additional damaged specimen of uncertain sex from the type locality. It possibly represents the female of this species and possesses pale halteres, in contrast to the dark halteres of males (similar sexual dimorphism observed in *A. apicalis*).

### ***Acarterus stuckenbergi* sp. n.**

Figs 20, 21

*Etymology*: Named in honour of Brian Stuckenberg in recognition of his dedication to the study of South Africa dipterology.

Holotype ♂: SOUTH AFRICA: *Cape Province*: 'Naudes Nek/ Barkly East Dist./ East. Cape Prov./ 2350–2525 m./ 19 Jan. 1963 [B. & P. Stuckenberg]'; 'HOLOTYPE/ *Acarterus/ stuckenbergi/ Sinclair*' [red label]. In NMSA.

*Recognition*: Distinguished from other small, dark species of *Acarterus* by the slightly swollen hind femora with stout anteroventral setae on the apical third and by a hind tibia much shorter than the femur and swollen apically.

*Description* (male): Wing length 2.6 mm.

**Head:** First flagellomere more than twice as long as pedicel and scape combined; arista 1.25 times longer than first flagellomere. Proboscis slightly longer than height of head.

**Thorax:** Brown, apex of postpronotal lobe yellowish-brown; dusted with pruinescence; vittae lacking. Setulae long, slender; acrostichal setulae in 4 rows, 1 pair of setae on either side of prescutellar depression; dorsocentral setulae uniserial, with 2 postsutural dorsocentral setae; 4 intra-alar setulae; 1 postpronotal, with several long, fine setulae; 4 notopleurals; 1 postalar; 3 pairs scutellar setae. Anteprenotum with row of long setae. Halter dark.

**Legs:** All segments concolorous with pleura. Tibiae with several long setae. Hind femur nearly 1.5 X longer than mid femur, somewhat thickened, bearing several stout anteroventral setae on apical third; anteroventral margin with row of long setae. Hind tibia straight, slightly shorter than femur, apex swollen. Hind coxae broader than mid coxae.

**Wings:** Stigma distinct, elongate;  $R_1$  straight; remnant of  $M_1$  not visible;  $CuA_1$  1.25 X length of crossvein dm-cu;  $CuA_2$  convex, meeting  $A_1$  at right angle.

**Abdomen:** Lateral and ventral margins with long, pale, silky setae; concolorous with thorax, dusty with grey pruinescence; lacking bands of pruinescence.

**Terminalia** (Figs 20, 21): Right surstylus narrow, tapering to blunt tip with short apical tooth and single setula; right surstylus lacking basal lobe; left surstylus broad, tapering, bearing 2 apical teeth and single setula; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe strongly attenuated, slightly longer than left lobe; left hypandrial lobe with broad base, tapering to round apex. Left postgonite with expanded apex, extending dorsally over phallus; right postgonite slender and short.

**Female:** Unknown.

**Remarks:** See remarks under *A. pallidus* regarding the vegetation of the type locality. These species are from high altitudes and have a phenological range limited to mid-summer.

### ***Acarterus unicolor* Loew**

Figs 22–25

**Holotype** ♂: SOUTH AFRICA: *Cape Province*: ‘Cap. B/ Spei.’; ‘Victo-/rin’; ‘135.’; ‘134.’; ‘*Acarterus/ unicolor*’. In NRS.

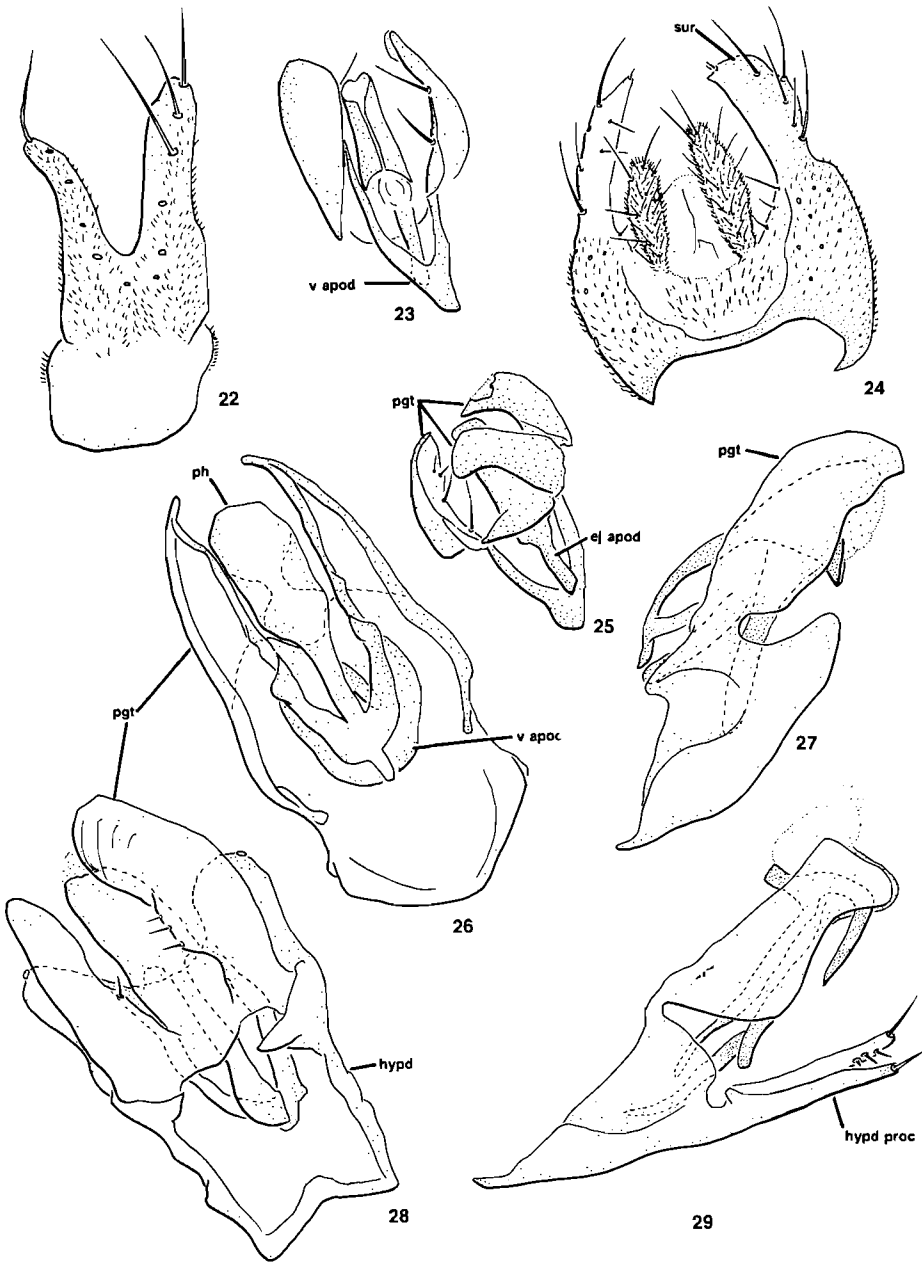
**Recognition:** This species is distinguished by its small size, dark coloration and dark unmodified hind femora. Refer to ‘Recognition’ section under *A. macrochaetus* and *A. nigricans*.

**Description (male):** Wing length 2.0–2.5 mm.

**Head:** First flagellomere twice as long as pedicel and scape combined; arista slightly shorter to slightly longer than first flagellomere. Proboscis slightly shorter than height of head.

**Thorax:** Brown to black, including apex of postpronotal lobe; dusted with pruinescence; vittae lacking. Setulae short; acrostichal setulae in 4 rows, lacking setae on either side of prescutellar depression; dorsocentral setulae uniserial, with 2 postsutural dorsocentral setae; intra-alar setulae in 3–4 rows; 1 postpronotal, with





Figs 22–29. Male terminalia of species of *Acarterus*, *Lamachella*, *Bicellaria* and *Stenoproctus*. 22–25. *A. unicolor* Loew. 22. Hypandrium, ventral view. 23. Postgonites and phallus, ventral view. 24. Epandrium and cerci, dorsal view. 25. Postgonites and phallus, dorsal view. 26–27. *L. marginalis* Smith. 26. Hypandrium, phallus and postgonites, dorsal view. 27. Hypandrium, phallus and postgonites, lateral view. 28. *S. venaticus* Smith, hypandrium, phallus and postgonites, dorsal view. 29. *Bicellaria* sp., hypandrium, postgonites and phallus, lateral view. [Abbreviations: ej apod = ejaculatory apodeme; hypd = hypandrium; hypd proc = hypandrial process; pgd = postgonite; ph = phallus; sur = surstylus; v apod = ventral apodeme.]

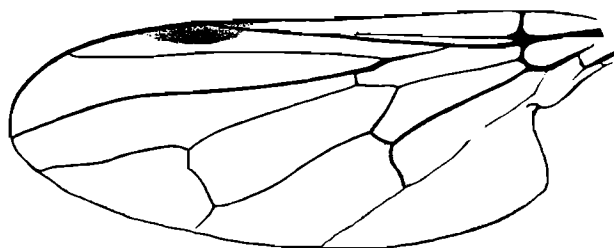
many long, fine setae; 3–4 notopleurals; 1 postalar; 4–5 pairs scutellar setae. Anteprenotum with row of long setae. Halter dark.

Legs: All segments brown to black, lacking stout setae. Tibiae with several long setae. Hind femur slightly longer than mid femur, not thickened; anteroventral margin with row of long setae. Hind tibia straight, subequal in length to femur, apex not swollen. Hind coxae subequal in width to mid coxae.

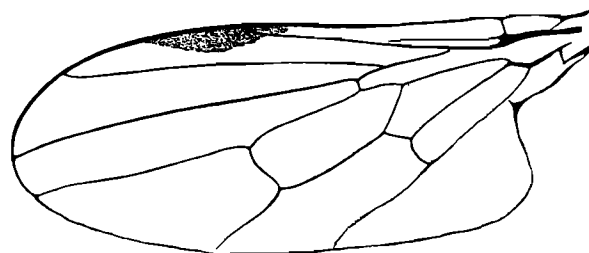
Wings: Stigma distinct, elongate;  $R_1$  straight; remnant of  $M_1$  not visible;  $CuA_1$  at most twice length of crossvein  $dm-cu$ ;  $CuA_2$  convex, meeting  $A_1$  at right angle.

*Abdomen*: Lateral margin with long, dark setae; concolorous with thorax, dusty with grey pruinescence; lacking bands of pruinescence.

*Terminalia* (Figs 22–25): Right surstylus broad, flattened, tapering to point bearing short peg-like seta; right surstylus lacking short, basal lobe; left surstylus dorsoventrally flattened, apex rounded, with 1 subapical lateral tooth and several setulae; surstyli bare, lacking microtrichia, surface polished. Right hypandrial lobe straight, broad, longer than left lobe; left hypandrial lobe slender, gradually arched apically. Left postgonite with pair of lateral processes extending dorsally over phallus; anterior process broad, posterior process with subapical notch; right postgonite slender with round apex.



— 30



— 31

Figs 30–31. *Acarterus* species, wings. 30. *A. londti* sp. n. 31. *A. nigricans* sp. n. [Scale bars = 0.5 mm.]

Female: Similar to male except for abdomen. See generic description.

Additional material (collectors B. & P. Stuckenberg): SOUTH AFRICA: *Cape Province*: 1 ♀, Bainskloof, Wellington Dist., 2000', 4–5.x.1959 (NMSA); 1 ♂ 1 ♀, Du Toits Kloof/ Paarl Dist., 2000–3500', 27–28.xi.1959 (NMSA); 1 ♂ 2 ♀, Nieuwoudtville area, Calvinia District, 14.x.1964 (NMSA); 1 ♂, Pakhuis Pass, Clanwilliam Dist., 17–19.x.1964, 950m (NMSA); 6 ♂ 3 ♀, Sevenweekspoort, Laingsburg Dist., 19–22.xi.1959 (NMSA). 1 ♂ 1 ♀ deposited in CNC.

Remarks: The female holotype is in excellent condition and despite the difficulty in associating the sexes, I concur with Smith (1969) that the additional material examined is conspecific. There were three small dark species (*unicolor*, *macrochaetus*, *nigricans*) matching the description of *A. unicolor*, but its identification was confirmed based on its thoracic chaetotaxy and the size of the thorax.

This species appears to be widespread throughout the southwestern Cape Province (Fig. 32). Adults have been active in the spring, and have been found in mesic Montane Fynbos.

#### Undescribed Species

Although each of the following species is distinct, I am reluctant to formally name them until associated males are collected.

##### *Acarterus* sp. 1

Material examined: SOUTH AFRICA: *Cape Province*: 1 ♀, Jonkershoek For. Res. 33°58'S:18°55'E, 30.ix.1993, J. G. H. Londt, mountainside macchia, 240 m (NMSA).

Recognition: Distinguished from other species by its large size (wing length 4.3 mm), coxae concolorous with thorax, pale halter, and swollen hind femur with a distinct apical band and stout ventral setae.

##### *Acarterus* sp. 2

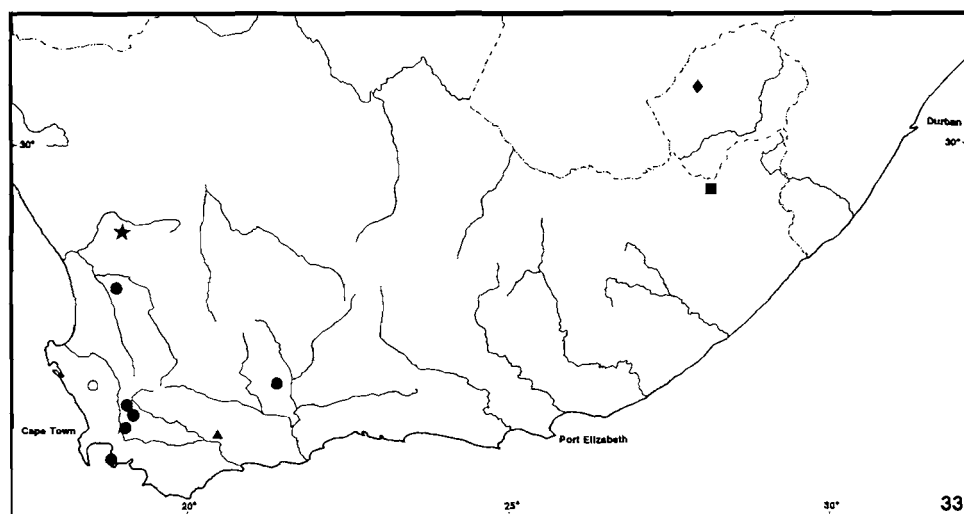
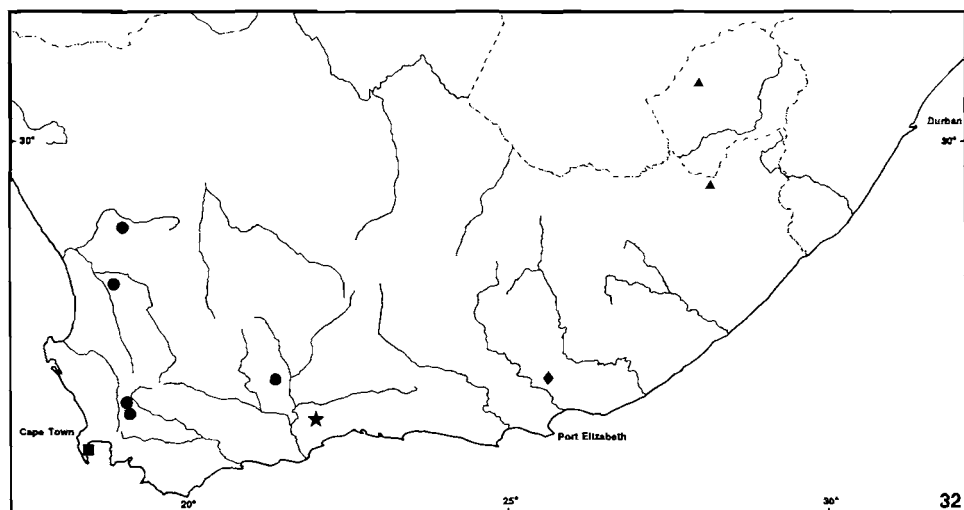
Material examined. SOUTH AFRICA: *Cape Province*: 1 ♀, Nieuwoudtville area, Calvinia District, 14.x.1964, B. & P. Stuckenberg (NMSA).

Recognition. Distinguished from other species of *Acarterus* by its medium size (wing length 3.1 mm), black coloration, silver pair of scutal vittae, long thoracic setae and biserial acrostichals, pale halter, and swollen hind femur with biserial row of stout setae beneath.

##### *Acarterus* sp. 3

Material examined. LESOTHO: 1 ♀, Blue Mountain Pass, Makhaleng Valley, Maloti Mountains, Maseru District, 12–14.i.1963, , B. & P. Stuckenberg, 2150–2525 m (NMSA).

Recognition. Distinguished from other species of *Acarterus* by its small size (wing length 2.6 mm), greyish body and legs, pale halter, biserial acrostichals, and unmodified hindlegs.



Figs 32–33. Known distribution of species of *Acarterus*. 32. ● = *A. unicolor* Loew, ■ = *A. darwini* sp. n., ▲ = *A. pallidus* sp. n., ◆ = *A. apicalis* sp. n., ★ = *A. nigricans* sp. n. 33. ● = *A. londti* sp. n., ▲ = *A. macrochaetus* sp. n., ■ = *A. stuckenbergi* sp. n., ○ = *A. sp. 1*, ★ = *A. sp. 2*, ◆ = *A. sp. 3*.

#### PHYLOGENETIC CONSIDERATIONS

##### Phylogenetic position of *Acarterus* within Hybotinae

The Cretaceous fossil *Pseudoacarterus* Waters, 1989, appears very similar to, if not congeneric with an expanded definition of *Acarterus*. Waters (1989) considered the fossil to be ancestral to *Syndyas* on the basis of a reduced M vein separating the basal cells and a thickened hind femur. However, vein M does not appear reduced to the extent observed in *Syndyas* (c.f. Waters 1989, fig. 3; Smith 1969, fig. 121). In addition, vein Rs in *Pseudoacarterus* is long, arising basal to the middle of cell bm, while it is quite short in *Syndyas*. Consequently, on the basis of a long vein Rs and

thickened hind femur, it is possible that *Pseudoacarterus* and *Acarterus* are most closely related.

The phylogenetic position of *Acarterus* within the Hybotinae remains debatable. *Acarterus* has a long proboscis, similar to that of *Syneches*, but the proboscis in the former genus is more slender and the labella remain distinct, bearing pseudotrachea. The male terminalia of *Acarterus* differ greatly from those of *Syneches*, but are most similar to that of *Stenoproctus* and *Afrohybos*. However, this similarity is probably based on symplesiomorphies. The genera of the Hybotinae may be divided into the following four groups:

1. *Hybos*-group (*Ceratohybos* Bezzi, *Euhybus* Coquillett, *Hybos*, *Lactistomyia* Melander, *Syndyas*).  
This group is characterised by a largely tubular phallus (Chvála 1983, fig. 170), reduced ventral apodeme, shortened postgonites, and short Rs arising distal to the middle of cell bm.
2. *Syneches*-group (*Syneches* s.l., *Parahybos* Kertész).  
This group is characterised by a flattened head.
3. *Stenoproctus*-group (*Chillcottomyia*, *Lamachella*, *Stenoproctus*).  
This group is characterised by a shortened cell cup (anal cell) with a truncate apex, well-developed ventral apodeme, phallus with a hood-like apex, conical first flagellomere, and well-developed postgonites. Cell cup is similar in shape to that of the Ocydromiinae, but is likely a result of convergence. A shortened cell cup is considered a derived feature, as suggested by Hennig (1970).
4. *Afrohybos*-group (*Afrohybos*, undescribed genus).  
This group is characterised by a swollen hind basitarsus, apically swollen hind tibia, and a short unmodified proboscis, bearing pseudotracheae (also present in *Euhybus* and *Acarterus*).

The *Hybos* and *Syneches*-groups are possibly most closely related on the basis of a short-ovate first flagellomere. However, the relationships among the remaining groups and the position of *Acarterus* remain unresolved.

#### Reconstructed Phylogeny of the species of *Acarterus*

Six morphological characters were used in the phylogenetic analysis to resolve the relationships between species of *Acarterus*. In the following discussion of characters, the italicised words following a character number describe the apomorphic state of the character under consideration and the numbers correspond to those used in the cladogram (Fig. 34). The remaining hybotine genera are used to represent a generalised outgroup.

1. *Left postgonite with single lobe arched over tip of phallus*.  
In the outgroup (e.g. *Stenoproctus* and *Lamachella*), the postgonites are fairly straight and do not arch dorsally over the phallus (Figs 26, 28). The left postgonite comprises a single lobe in three species (Figs 1, 19, 21).
2. *Hind femur slender*.  
The hind femur is considered to be thickened in the ground plan of the Hybotinae (Fig. 8). A shift to a slender hind femur is hypothesised to have

evolved independently in both *A. pallidus* + *A. stuckenbergi* and *A. nigricans* + *A. macrochaetus*.

3. *Left postgonite subdivided.*

The left postgonite in *A. pallidus*, *A. stuckenbergi*, and *A. apicalis* is undivided (Figs 1, 19, 21). In the remaining species of *Acarterus*, the left postgonite is subdivided into various lobes and the lower lobe is arched dorsally over the phallus (Figs 5, 14, 16, 25).

4. *Left surstylus broad with subapical teeth.*

The left surstylus is undifferentiated in the ground plan of *Acarterus* and other hybotines (Fig. 2). The left surstylus is broad with subapical teeth in four species of *Acarterus* (Fig. 24).

5. *Base of right surstylus with short lobe.*

A short lobe at the base of the right surstylus is lacking in most species of *Acarterus* and most hybotine genera. This synapomorphy occurs in three species of *Acarterus* (Figs 10, 14, 16).

6. *Lower lobe of left postgonite reduced to slender lobe.*

The lower lobe of the left postgonite is broad in *A. darwini*, *A. unicolor*, and *A. londti*. The lower lobe of the left postgonite is slender in *A. nigricans* and *A. macrochaetus* (Figs 14, 16).

The cladistic analysis executed with Hennig86 (Farris 1988) produced one equal-length tree, presented here using Clados (Nixon 1992) to facilitate the printed output (Fig. 34). The resulting tree divided the species into a western Cape Province group and an eastern Highlands group. This latter group also includes a species from the eastern Cape Province (see below). Species from the eastern Highlands group were collected during mid-summer (January), except for the species from the eastern Cape Province (*A. apicalis*) which was collected in Autumn (April). Species from the western Cape Province group were collected primarily during spring (September/October), except *A. darwini* which was collected in winter (June) and *A. macrochaetus* collected in summer (February).

The undescribed species were not included because mostly male genitalic characters were used in the analysis. With the discovery of corresponding males, these species could be used to test the validity of the proposed species groups and inter-relationships. However, on the basis of geographic distribution it is predicted that undescribed sp. 3 will be most closely related to the eastern Highlands group and undescribed spp. 1 and 2 will be most closely related to the western Cape Province group.

#### ZOOGEOGRAPHY

More extensive collecting of *Acarterus* has revealed that it is distributed beyond the southwestern Cape (Figs 32, 33) as discussed by Smith (1969). *Acarterus* can be divided into two main centres of diversity: (1) the southwestern region of the Cape Province and (2) the eastern Highlands. This latter group includes a species from the Suurberg range (eastern Cape Province) which represents an area transitional between the two main centres (Stuckenberg 1962). These regions were probably

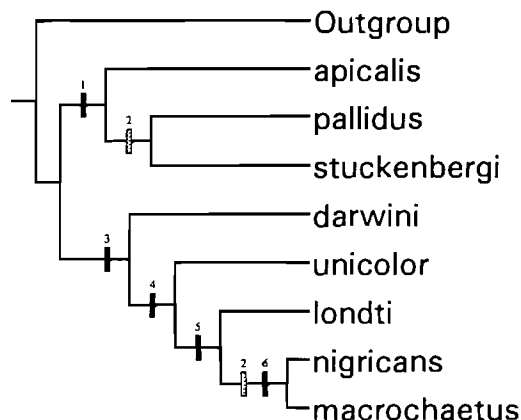


Fig. 34. Hypothesised cladistic relationships of the species of *Acarterus*. Numbers refers to characters discussed in the text.

separated during the increasing aridity of the Miocene. The distribution of *Acarterus* is also very similar to genera of the Rhagionidae (Stuckenberg 1962, fig. 5).

The southwestern Cape exhibits an astonishing diversity of fauna and flora (Stuckenberg 1962). There are also a greater number of species of *Acarterus* in this region than the eastern Highlands. This overall greater diversity is believed to be due to a combination of factors, including varied landscape, varying rainfall, and rainshadow effects. This region experiences mostly winter rains and dry summers and the eastern Highlands receives spring rains (Stuckenberg (1962).

The distribution and possible age of *Acarterus* suggests that it is an example of a palaeogenic element and represents an ancient, relict taxon. Given its probable close relationship to *Pseudoacarterus* and apparent absence from southern South America, it is hypothesised that *Acarterus* was established by the Late Cretaceous [87.7–95.4 mya (Waters 1989)], following the separation of southern Africa from South America.

#### ACKNOWLEDGEMENTS

I would like to thank D. A. Barraclough (NMSA) and J. Chainey (BMNH) for the loan of specimens of *Acarterus* and B. Viklund (NRS) for the loan of the holotype of *A. unicolor*. K. G. V. Smith kindly confirmed the authenticity of the Darwin specimens and provided additional background information. J. M. Cumming (CNC) and B. R. Stuckenberg (NMSA) kindly reviewed earlier drafts of this paper. Brian Stuckenberg also added extensive supplemental habitat data. This research was partially supported by a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada.

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